Evolutionary aspects of development, life style, and reproductive mode in incirrate octopods (Mollusca, Cephalopoda)*

by

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With 7 figures

ABSTRACT

The incirrate octopods are defined as a monophyletic group by a number of characters unknown in the cirrate octopods or in other cephalopods. The biologically most significant incirrate feature is the incubation of eggs by the female. The morphological and behavioural characters underlying this special mode are analysed with regard to developmental processes and their modification related to life style evolution.

1. INTRODUCTION

Common inshore species of the genus *Octopus* Lamarck, 1798 are popular models in comparative invertebrate biology (YOUNG, 1971; WELLS, 1978); in such a context they can be viewed as 'typical cephalopods'. When attention is focussed on diversity *within* the class Cephalopoda, however, the common octopuses turn out to be rather 'special' cephalopods. This observation raises the question of respective systematic positions: what is special about which group of octopods ?

1.1. SYSTEMATICS

Within the cephalopod subclass Coleoidea Bather, 1888 (=Endocochleata, Dibranchiata), the order Octopoda Leach, 1818 is a well defined taxon. It contains two suborders, the Cirrata Grimpe, 1916 (better known as 'finned octopods') and the Incirrata

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Grimpe, 1916, to which the common octopuses belong. YOUNG (1989) proposed a new classification, with an infraclass Octobrachia containing two orders, the Cirroctopoda (=Cirrata) and the Octopoda (=Incirrata). For practical reasons, the old classification is used here, especially to avoid confusion between Octopoda Leach, 1818 and Octopoda Young, 1989 (cf. quotation from YOUNG, loc. cit. in Discussion).

1.2. PHYLOGENETIC BACKGROUND

To appreciate the evolutionary significance of incirrate characters with regard to functional adaptation and phyletic conservation of patterns, the incirrates must of course be viewed in comparison to their supposedly closest relatives, the deap-sea cirrate octopods. The respective positions of the fossil *Proteroctopus* of the Middle Jurassic and *Palaeoctopus* of the Late Cretaceous are not discussed here, because the available morphological data are insufficient (see ENGESER, 1988 for a review). The characters of living octopods can nevertheless be scrutinized in the greater framework of coleoid phylogeny, starting out from the Vampyromorpha (cf. YOUNG, 1989). This taxon was formerly included in the Cirrata because of the great similarity in arm morphology. When the so-called retractile filaments of *Vampyroteuthis* were recognized as an additional pair of rudimentary arms, the Vampyromorpha were made an order of its own (PICKFORD, 1939, 1949).

The evolutionary history of endocochleate cephalopods can be traced back to the lower Devonian (BANDEL *et al.* , 1983; BANDEL & BOLETZKY, 1988). For the present purpose it is sufficient to consider the extant coleoids in relation to those fossil coleoids that had *ten arms of similar length and structure*, a crucial feature that NAEF (1923) used for the definition of a hypothetical 'Protodibranchus'. This arm pattern disappeared with the extinction of the belemnites at the end of the Cretaceous.

The 'belemnoid' arm crown morphology is important for our understanding of coleoid phylogeny because it is the only one from which one can derive the respective patterns of 1) the decapodan cuttlefishes and squids, which have the *fourth arm pair modified* as tentacles, and 2) a group provisionally named 'Vampyropoda' (=Octopodi-formes Berthold & Engeser, 1987; name preoccupied) to include the Vampyromorpha Pickford, 1939 with their *modified second arm pair* and the Octopoda Leach, 1818 (lack of probably the second arm pair). The important point here is that these two modifications must have occurred independently, i. e. at two different speciation events, because a simultaneous occurrence of mutually exclusive modifications is inconceivable (Fig. 1a). Prerequisite to this phylogenetic deduction is the existence of unambiguous identities and positional relationships of brachial appendages allowing one to recognize modifications for a given pair of arms (see BOLETZKY, 1992 for a review). These criteria are concerned with the 'integration level' of distinct appendages; they do not involve the specialisations at the next lower level which comprises the armature of the arms and tentacles (suckers, hooks, cirri).

Given the situation described above, any discussion of phylogenetic systematics of the Coleoidea has to cope with (only) two possibilities: either the decapods and the belemnoids are sister groups for which the 'Vampyropoda' are the outgroup, or the 'Vampyropoda' and the belemnoids are sister groups, the decapods being the outgroup (Fig. 1b). The question of which one of these arrangements is true lies outside the scope of this paper.

2. INCIRRATE CHARACTERS

In addition to the absence of brachial cirri warranting the name of the taxon, and hectocotylization of one of the ventro-lateral arms, the Incirrata show a series of characters unknown in the Cirrata or in any other coleoid cephalopod (cf. NAEF, 1923, 1928); the most conspicuous of these are:

1. absence of muscular fins ('finlessness')
2. presence of Kölliker's organs in hatchling skin
3. partial modification of egg case (chorion stalk)
4. reduced encapsulation of egg case (chorion stalk only)
5. egg-care behaviour (or ovovivipary) in the female.

Although none of these characters is known in any other cephalopod, the question remains whether they are uniquely derived (apomorphic) characters of the Incirrata, or whether they (or some of them) could be autapomorphic characters of the octopodan ancestor that were subsequently eliminated in the Cirrata (so they would be plesiomorphic at the level of the Incirrata). So far nothing seems to indicate that the absence of the above characters in the Cirrata could be the result of such an elimination.

An equally important question is how closely related these characters are to one another. Here one has to consider several variables; a behavioural one, namely the post-hatching life style as compared to the adult mode of life, and two morphometrical variables, egg size and body proportions. The behavioural features necessarily lead to the question of how to define the ancestral life style from which the modes of living incirrates must be derived. Before this question can be addressed, the incirrate characters listed above have to be scrutinized in some detail.

Ad 1. The absence of muscular fins in the Incirrata is not total if embryonic development is taken into account. Fin rudiments do appear during organogenesis, in close positional relation to the shell sac as is typical for the coleoids (Fig. 2). The incirrate shell sac is very small from the beginning; it becomes drawn out laterally during early development (APPELÖF, 1898). The resulting transverse tube finally splits into two independant tubes which become embedded in the muscular tissue of the mantle (and can finally disappear, as in *Argonauta*). During this shell sac differentiation the fin rudiments gradually smooth out (NAEF, 1928). What might be taken as rudimentary fins in preserved hatchlings viewed in the scanning electron microscope are fixation artefacts due to shrinkage (Fig. 3); although the position of these ostensible 'buds' corresponds to the location of the shell stylets, no trace of fin tissue is histologically detectable. The character 'absence of muscular fins' could be rephrased to emphasize the rudimentation of the whole fin-shell complex, assuming homology of fin *rudiments* in Cirrata and Incirrata (BOLETZKY, 1982 a). When viewed against the pattern of an unpaired transverse shell sac and associated fins (as present in cirrates), the bipartite shell sac of incirrates suggests a correlation between two apomorphic characters, namely subdivision of the shell sac and truncation of fin differentiation, i. e. 'finlessness'.

Ad 2. The majority of incirrate hatchlings have special tegumentary organs; they were observed in *Argonauta* embryos by KÖLLIKER (1844) and fully described in other incirrates by QUERNER (1927) and more recent authors (e. g. FIORONI, 1962) (Fig. 3). The absence of Kölliker's organs in *Octopus briareus* (Fig. 7) and *O. maya* (BOLETZKY, 1973)

can be viewed as the result of total suppression in specifically modified integument morphogeneses. So far no trace of these organs has been found in embryos of cirrate octopods (BOLETZKY, 1982 b).

Ad 3. During vitellogenesis, cephalopod oocytes may take on a markedly elongate form, but it is only in the Incirrata that this elongation leads to the differentiation of a distinct chorion stalk (Figs 4, 5). The elongate form of the incirrate chorion is also meaningful with regard to embryonic movements that occur in all incirrates so far studied, with the exception of *Argonauta* ; this feature could be a side effect of the primary modification of late oogenetic processes (BOLETZKY & FIORONI, 1990) (Fig. 4).

Ad 4. In the incirrates the 'cement' secreted by the oviducal glands (FROESCH & MARTHY, 1975) 'encapsulates' only part of the chorion stalk (Fig. 5). This 'partial egg encapsulation' contrasts with the complete encapsulation of the cirrate eggs; it thus appears as an apomorphic character linked with the formation of a chorion stalk (character 3).

Ad 5. Although visual stimulation by other egg masses can induce spawning in many coleoid cephalopods,   post-spawning *egg care* exists only in the incirrate octopods (BOLETZKY, 1986). This unique protective behaviour must be related to the *absence* of protective encapsulation (character 4). In other words, characters 3, 4 and 5 are clearly connected, forming an apomorphic complex of features named the "incubating mode" of reproduction. In the pelagic genus *Ocythoe*, incubation exists in the 'pure' form of ovovivipary (NAEF, 1923). For two families, the Alloposidae and the Amphitretidae, egg-care is not yet documented (Hochberg, pers. comm.).

Before approaching the question of possible relations between the above 'incubation complex' and the characters 1 and 2 (see **C.**), it is necessary **A.** to review life styles and morphometrics at different stages of the incirrate life cycle, and **B.** to see whether characters 1 and 2 are correlated.

A. LIFE STYLES AND MORPHOMETRICS

A.1. Life styles

a) ADULT LIFE STYLES IN THE INCIRRATA

Eight incirrate families are recognized if the Idioctopodidae Taki, 1962 are included in the Amphitretidae Hoyle, 1886 (cf. HOCHBERG *et al.*, 1992; disregard the erroneous statement in BOLETZKY, 1978-79, p. 107). Only the Octopodidae Orbigny, 1840 are clearly benthic at the adult stage. R. E. YOUNG (pers. comm. to HOCHBERG *et al.*, 1992) suggests that adult *Alloposus mollis* Verrill, 1880 (of the monotypic family Alloposidae Verrill, 1882) may also be benthic. The remaining six families are pelagic; these are the Argonautidae Tryon, 1879, the Tremoctopodidae Tryon, 1879, the Ocythoidae Gray, 1849 (these three families were grouped with the Alloposidae in a tribe called Argonautida by ROBSON, 1932), the Vitreledonellidae Robson, 1930, and the two "ctenoglossan" families Bolitaenidae Chun, 1911 and Amphitretidae Hoyle, 1886.

In all these families, reproduction takes place in midwater, and the eggs apparently remain with the female until the young hatch out. The most elaborate mode of egg care is achieved by the female *Argonauta* which produces a calcified "brood shell". However, along with housing the egg mass, this pseudoconch serves as a floater; the animal keeps an air bubble in the apex and thus obtains neutral buoyancy (BOLETZKY, 1983). Moreover the brood shell supports the brachial membrane in a food detective function (YOUNG, 1960). A much simpler form of egg carrier is produced by *Tremoctopus* ; as in *Argonauta*, the calcified structures are secreted by the dorsal arms (NAEF, 1923). In *Eledonella pygmaea* (family Bolitaenidae), the whole arm crown of the female forms a brood chamber (YOUNG, 1972). Male sexual behaviour in pelagic incirrates can be only partly inferred from the structure of the copulatory arm (hectocotylus). In the "Argonautida" *sensu* ROBSON (1932), the morphologically and morphometrically extreme differentiation of the hectocotylus seems correlated with the capacity to autotomize.

In the benthic Octopodidae, females always spawn on the bottom. Generally single eggs or egg strings are cemented to the wall or ceiling of the den occupied by the female. In a few octopodid species, the females carry egg masses loose and thus can move about while brooding the eggs (see HOCHBERG *et al.*, 1992).

b) POST-HATCHING LIFE STYLES IN THE INCIRRATA

As far as is known (cf. HOCHBERG *et al.*, 1992), the juveniles of pelagic families live in midwater (including the Alloposidae; see above). In the benthic Octopodidae, the representatives of the subfamily Bathypolypodinae Robson, 1931 probably stay on the bottom throughout their life (cf. *Bathypolypus arcticus*, as observed by O'DOR & MACALASTER, 1983). If the new arrangement proposed by VOSS (1988) is accepted, the new subfamilies Graneledoninae and Pareledoninae are entirely holobenthic (Hochberg., pers. comm.). The subfamilies Octopodinae Grimpe, 1921 and Eledoninae Gray, 1849 include numerous species characterized by the same 'holobenthic' mode as *Bathypolypus*, while others have a planktonic post-hatching phase; the mode of life of the latter species can be named 'merobenthic'. Their young animals are actively foraging carnivores that feed on both living planktonic prey and drifting food items (facultative scavenging). They generally remain in midwater until they have grown larger. In some species, newly-hatched animals show temporary settling between phases of active swimming (BOLETZKY, 1977).

A.2. Morphometrics

a) BODY PROPORTIONS OF INCIRRATE HATCHLINGS

The hatchlings of pelagic incirrates are characterized by short arms (generally less than 1/3 of total length) with few suckers. This feature again appears in the newly hatched animals of merobenthic octopodids (Fig. 6), although in the larger hatchlings each of these relatively short arms may carry up to 15 suckers. In contrast, the hatchlings of holobenthic octopodids have arms at least as long as the rest of the body, with more than 20 suckers per arm (Fig. 7).

The body proportions of planktonic hatchlings gradually change due to the positive allometric growth of the arms. In the young merobenthic octopodids, body proportions thus become similar to those of the 'crawl-away' hatchlings of holobenthic species. In *Octopus vulgaris* (and probably in the majority of merobenthic octopodids) the young animals, having reached these body proportions, gradually change from continuous swimming to the adult-type bottom life, which includes only occasional excursions into the water column (ITAMI *et al.*, 1963). This drastic change contrasts with the condition of pelagic incirrates, in which juvenile arm growth is not accompanied by a thorough modification of life style.

b) INCIRRATE EGG SIZES AND HATCHLING FEATURES

Within the Incirrata, the size of a single ovum varies from 0.8 mm in *Argonauta* spp. to 35 mm in *Graneledone* sp. (HOCHBERG *et al.*, 1992). Among the pelagic incirrates, the variation spans only from 0.8 to about 4 mm, however. In contrast, egg sizes vary from about 1.5 mm to 35 mm in the Octopodidae.

ROBSON (1932, p. 25) once expressed egg lengths as percentages of adult mantle-lengths, but his erroneous egg index for *Eledone cirrosa* prevented him from realizing the great difference between *Eledone moschata* (egg length ca 15% of adult mantle length) and *E. cirrhosa* (ca 5%; cf. Fig. 5); adults of the two species are similar in size. This index becomes particularly interesting when absolute egg sizes are similar among species with very *different adult sizes*. There are several octopodid species that produce eggs measuring about 5 to 8 mm; in the larger species the embryos become planktonic hatchlings with short arms and less than 15 suckers per arm, whereas in the smaller species embryos of the same size end up as benthic hatchlings with long arms and more than 20 suckers per arm (cf. A.2.a). In fact, the ostensibly 'intermediate' egg sizes fall under the same categories as the 'very large' and the 'very small' eggs and are distinguishable by the *relative* egg size, or egg index (BOLETZKY, 1974, 1977). An index smaller than 10% is indicative of the merobenthic mode, whereas an index greater than 10% reflects holobenthic conditions (occasional behavioural peculiarities in newly hatched animals notwithstanding). An exception is *Octopus fitchi*, a very small species in which the eggs (ca 5 mm) are large relative to the adult mantle-length (ca 30 mm: egg index ca 16); the arms are stout and almost as long as the rest of the body like in hatchlings of holobenthic species, but each arm carries less than 17 suckers, and the post-hatching life style is clearly planktonic (HOCHBERG *et al.*, 1992).

B. CORRELATION OF CHARACTERS 1 AND 2

a) FINLESSNESS AND THE BENTHIC LIFE STYLE

That the incirrates lack fins was long interpreted as a result of adaptation to benthic life (NAEF, 1923). The absence of fins in the pelagic incirrates was then naturally viewed as a condition conserved from a finless benthic ancestor, assuming that fins lost in that ancestor were not "reinvented" in its pelagic descendants. However, a causal relationship between the benthic life style of an octopus and the absence of muscular fins has never been shown to exist. In fact, cuttlefish and sepiolid squids demonstrate that fins may be indispensable even on the bottom as can be seen when these animals bury in soft

substrates: at the outset of burying they can remain on the spot only because the fin movements counteract the propulsive effect of the funnel jet by which substrate particles are blown up. Fins can be expected to have disappeared from the morphogenetic program only if they were *incompatible* with the functional morphology corresponding to a given life style. There is no indication of such incompatibility in relation to the benthic life style as it appears in the Octopodidae.

b) FINLESSNESS AND THE PELAGIC LIFE STYLE

Among the pelagic incirrates, one condition may appear incompatible with the presence of fins; this is the presence of a brood shell in female *Argonauta*. However, one cannot reasonably assume that this highly elaborate female structure represents an ancestral incirrate condition. A feature really incompatible with the presence of fins could be character 2 of our list, i. e. presence of Kölliker's organs in the juvenile skin. The way these organs function, especially when they evaginate and spread the setal tufts, suggests that they would interfere with fin activity if fins still existed along with them. Provided that tuft spreading occurs under higher nervous control and has a parachute effect in midwater when the animal remains motionless (BOLETZKY, 1978-79), the establishment of Kölliker's organs can be considered in relation to the pelagic life style. At the level of the incirrate ancestor, this of course holds only for small body sizes at which the tufts can generate enough drag to slow sinking. In other words, the formation of Kölliker's organs is likely to reflect an originally *juvenile adaptation* to pelagic life. Finlessness thus appears as the obligatory counterpart of the juvenile 'setaceousness', in other words characters 1 and 2 of our list are probably correlated.

C. CORRELATION OF CHARACTER COMPLEXES

Nothing so far mentioned provides an indication of any relationship between the complex of characters 1 and 2 and the complex of characters 3, 4 and 5 of our list. Such a link appears only when *hatching* is considered. In the merobenthic and pelagic incirrates, Kölliker's organs play an essential, though passive, role during hatching (BOLETZKY, 1978-79). The setal cores of these organs provide a "shingle" structure to the hatchling skin and thus prevent its slipping back into the chorion when the animal makes the stretching movements necessary to work itself through the hatch opening (which is produced by enzymes released from the hatching gland). Notwithstanding exceptions like *Scaeurgus unicirrhus* where short arms are used during hatching (BOLETZKY, 1984), the role of the setal cores seems essential in the small young having very short arms that remain passive during hatching (in contrast to the holobenthic octopodids where the crawl-away hatchlings *always* use their long arms to work themselves out of the chorion). However, the shingle structure of the skin is effective only if the hatch opening has a solid edge. This condition is fulfilled by the relatively thick, stiff chorion of incirrate eggs.

Another question is whether this particular function during hatching is the primitive function of Kölliker's organs. The complex structure of these organs, especially the elaborate musculature that permits repeated spreading and retraction of the tufts during post-hatching life, and the fact that the organs cover also the arms where they are not needed for hatching, suggest that their function during hatching is a secondary adaptation

superimposed on a primary function related to the post-hatching mode of life. A prerequisite of this secondary adaptation must have been the modification of the encapsulation process, which changed from the complete encapsulation seen in the cirrates to partial encapsulation of the egg. This evolutionary transformation is conceivable only in combination with a special timing of egg release allowing the follicular chorion attachment to be drawn out into a distinct chorion stalk. Internal fertilization, a likely prerequisite, was already achieved in the octopodan ancestor, as demonstrated by the Cirrata (cf. VILLANUEVA, 1992); *Vampyroteuthis* appears to have external fertilization similar to the decapods (PICKFORD, 1949).

3. DISCUSSION

Starting from the feature 'finlessness' through the related 'setaceousness' and its implications in both the post-hatching life style and the hatching mechanism, our survey arrives at the question of the evolutionary origin of the incirrate mode of reproduction. Considering the constraints placed on egg shaping and timing of egg release, attention is naturally drawn to ovovivipary, the special incubation mode of *Ocythoe*. Could this mode represent the primitive condition from which the post-spawning egg care was derived? Is the inverse process more likely? Or is the 'intermediary' condition of *Argonauta*, where eggs are released only after the first cleavage stages (NAEF, 1928), closer to the primitive condition from which the other two were derived?

These questions inevitably raise the problem of the ancestral life style under which incubation became established. Given that seven of the eight living incirrate families are pelagic, it appears likely that the 'most generalized' life style represents the ancestral condition. But this hypothesis remains very vulnerable as long as it is only based on the respective numbers of extant families representing the pelagic or the benthic life style. An indication supporting the above hypothesis could be the existence of a pelagic juvenile phase in many octopodids (merobenthic species). This juvenile phase is likely to be a *conserved* feature that stems from a pelagic ancestor. Advantages of this conservation could have been greater availability of small prey animals in midwater (BOLETZKY, 1977, 1981) and low selective pressure in a relatively 'simple' open water environment where the limited behavioural repertoirs of very small juveniles suffice (BOLETZKY, 1987). Thus the planktonic juvenile phase would have been *eliminated* in the holobenthic species. It is indeed easier to imagine an evolutionary parallelism resulting from convergent suppressions of the pelagic phase than the inverse, namely independently emerging pelagic juvenile phases. With the latter hypothesis, it would be particularly difficult to explain why the planktonic hatchlings tend to be so similar, and why they resemble so closely those of the pelagic incirrates.

One may of course argue that perhaps the pre-octopodid ancestor was already characterized by juvenile life style switching; this would have allowed the holopelagic life cycle of the majority of incirrates to emerge through a paedomorphic 'abbreviation' by suppression of the ancestral adult mode. This could be the hypothesis underlying the comment of YOUNG (1989, p. 235-236) on a cryptic incirrate character related to the receptor system of the statocyst: "The division of the crista into nine sections is a unique apomorphic feature of the order Octopoda; it is not present in Cirroctopoda, which presumably never possessed it. The feature was possibly developed to provide for the wide

range of frequency of turning during walking and swimming. It is surprising to find that the crista is still so divided in all the pelagic octopods examined". The question can of course be reversed: is it surprising to find that the crista is so divided in all the pelagic incirrates ? Not if one assumes that the benthic octopodids are derived from a pelagic ancestor. Efforts should now be concentrated on the identification of sister group relationships within the incirrates. Do the octopodids have an immediate common ancestor with one of the other incirrate subgroups, or is the octopodid lineage derived from a basic dichotomy so that the Octopodidae were the sister group of all other incirrates ?

Two variants of a peculiar behavioural feature in some pelagic incirrates deserve special attention. One is the use of the own brood shell as a buoyant device by female *Argonauta* (cf. 2.A.1.a), the other is the use that male *Ocythoe* make of empty tests of doliolids and salps as drifting 'homes' (NAEF, 1923). The great similarity of these behavioural patterns suggests that the typical arm posture of a benthic octopodid sitting in its den is homologous to the respective attitudes of female *Argonauta* and male *Ocythoe* in their pelagic 'homes'. It is conceivable that the behaviour pattern corresponding to such a 'rafting' mode of life provided the initial condition for the establishment of an adult benthic mode. The inverse process seems conceivable only if the supposed benthic ancestor already had a planktonic juvenile phase.

In conclusion, the most generalized life style in incirrates is characterized by active swimming and drifting; ontogenetically this is an elaboration of a pelagic juvenile phase. This phase has probably been *eliminated* in many species of the benthic family Octopodidae. To derive the wide variety of incirrate modes from a holobenthic ancestor, through repeated 'invention' of the pelagic juvenile phase, seems rather problematic. Egg incubation in incirrates may thus be surmised to have emerged in the adaptive context of a bentho-pelagic or pelagic life style.

SUMMARY

This paper reviews the common features of the octopodan subgroup Incirrata from an evolutionary point of view, raising questions of functional adaptation and co-adaptation of morphological and behavioural characters. The most conspicuous difference between incirrate octopods and other cephalopods is the 'incubating mode' of reproduction (post-spawning egg care or ovovivipary). As the cirrate octopods, which are the likely sister group of the incirrates, show no signs of incubation, the evolutionary origin of this novel mode of incirrate reproduction can only be 'reconstructed' through careful weighing of the relative importance of characters that are more or less closely related to reproduction. Developmental features provide particularly interesting cues (e. g. truncation of fin development, formation of special tegumentary organs) allowing one to approach the question of the ancestral life style from which the pelagic and benthic modes of extant incirrates must be derived.

Decapoda   Vampyropoda

(Vampyromorpha + Octopoda)

Belemnoidea ext.

a

Decap. Belemn. Vampyrop.   Decap. Belemn. Vampyrop.
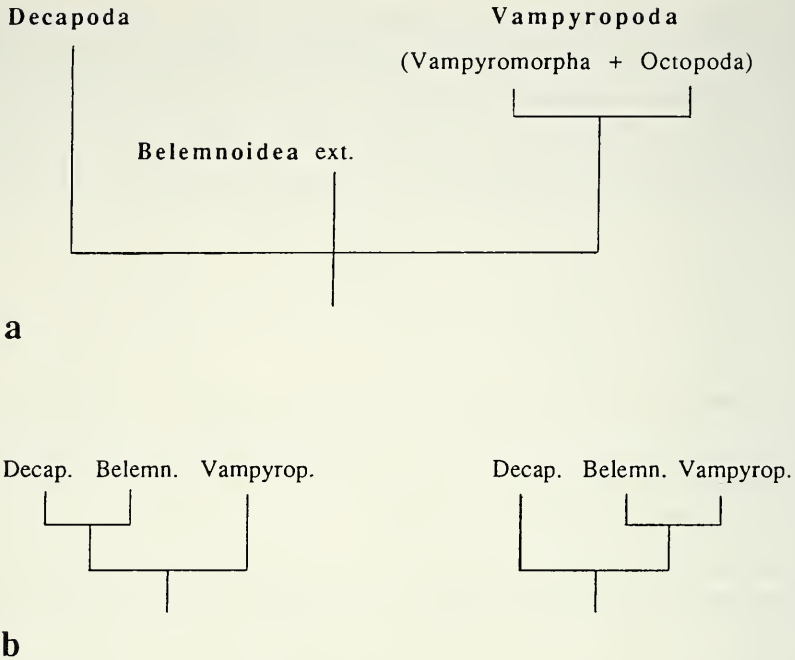
b

FIG. 1

a. Phylogenetic relationships between the living coleoid groups Decapoda (five arm pairs, fourth pair modified) and Vampyropoda (five arm pairs, second pair modified) via the extinct Belemnoidea (five arm pairs without distinct modifications). The trichotomy is shown unresolved in terms of sister group relationships. b. The two conceivable sister group relationships (the theoretical third one, supposing Decapoda + Vampyropoda with Belemnoidea as the outgroup, is inconceivable for morphological reasons, as explained in the text).

FIG. 2

Lateral view of a live embryo of *Octopus vulgaris* in its chorion, the large outer yolk sac (at right) and the chorion stalk (at left) are not shown. At this advanced organogenetic stage (stage XII of Naef, 1928), one can recognize the organ complexes surrounding the dark yolk mass: a voluminous buccal mass (b), the stubby arms (a), the funnel tube (f), and the cap-like mantle with the fin rudiments (arrow) overlying the rudimentary shell sac (arrow head).

FIG. 3

Preserved hatchling of *Octopus vulgaris* in caudo-dorsal view (SEM), with the posterior mantle apex at the lower left. The elevations marked by arrowheads correspond roughly to the position of fin rudiments in decapod embryos, but they are fixation artefacts due to shrinkage (see text). The small arrows point at some of the small elevations producing the "shingle" structure of the hatchling skin; the tips of the setal cores of Kölliker's organs have broken through the skin surface only in the nuchal region (upper right).
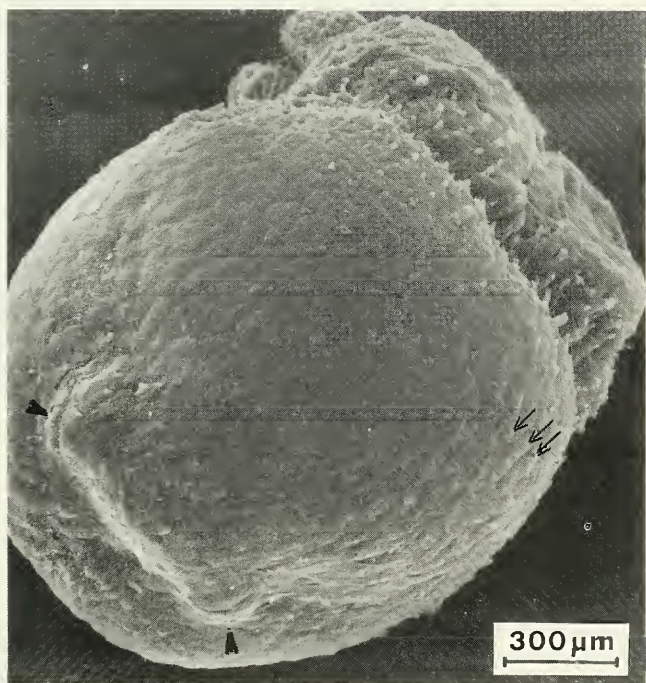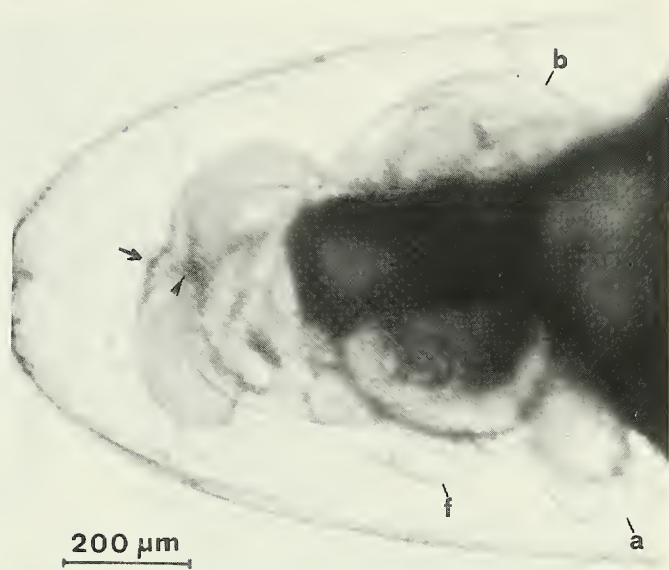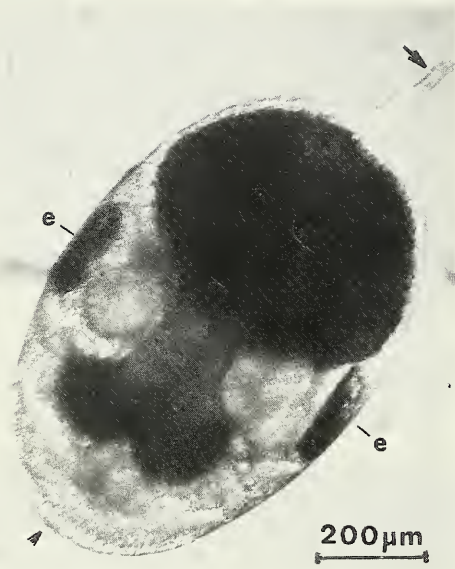
FIG. 4

Live embryo of *Argonauta argo*, with pigmented eyes (e), tightly enclosed in its chorion, with the chorion stalk (arrow) at the upper right. The outer yolk sac lies at the stalk side, the mantle of the embryo at the side of the micropyle (arrow head). At organogenetic stages, incirrate embryos normally show inverse orientation inside the chorion (see text).

FIG. 5

Egg strings from the octopodids *Eledone cirrhosa* (left and middle) and *Octopus vulgaris* (right). The arrow points at the embedding site of a long chorion stalk in the 'cement' secreted by the oviducal gland; the egg string in the middle shows a 'tidier' arrangement with deep chorion stalk embedding (arrow head) and formation of a central cement axis, similar to that of the *Octopus vulgaris* egg string (central axis not visible). Despite the great difference in egg size, hatchlings of both species have short arms (cf. Fig. 6) and live for some time in the plankton (see text).

1 mm

5 mm
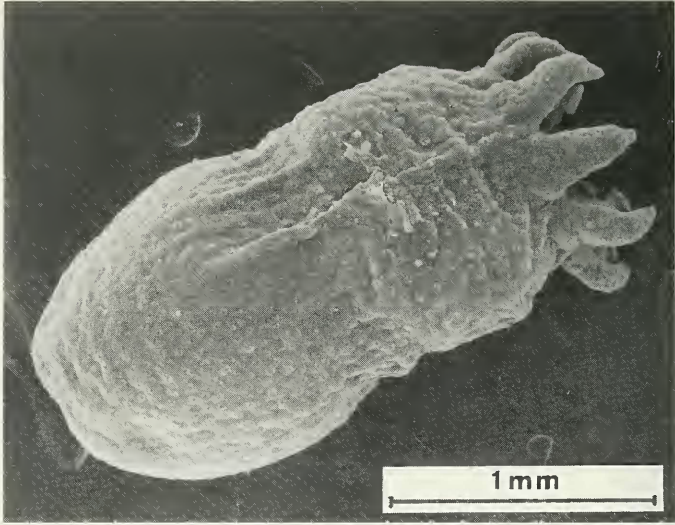
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FIG. 6

Scanning electronmicrograph of an *Octopus vulgaris* hatchling in dorsal view. Note the short arms with a few relatively large suckers (upper right).

FIG. 7

A live *Octopus briareus* hatchling with its long arms and numerous suckers adhering to the substrate (glass dish) during crawling. This is a bottom living 'miniature octopus' hatched from a very large egg, showing no signs of pelagic life style.

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